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GUY G. MUSSER¹

ABSTRACT

Limnomys is a genus of small rats represented by a handful of specimens from the Philippine Islands. Three species have been included within Limnomys: L. sibuanus, the type-species, and L. mearnsi, both from Mindanao; and L. picinus from Mindoro. I show in the present paper that mearnsi is likely only a geographic variant of L. sibuanus, and that the holotype of L. picinus is a

composite: the skin is that of a juvenile of Rattus mindorensis and the skull is from a specimen of Limnomys mearnsi. The content of Limnomys is then restricted to one species with possible geographic variants; that species is now known only from the mountains of Mindanao. Its possible relatives live in forests of Central Celebes.

INTRODUCTION

There are more than 30 species of endemic rats and mice that live in the primary forests of Central Celebes. Among these are Rattus beccarii and two undescribed species of small rats related to it. The three form a group that is distinct from any other species or group of species from Celebes or anywhere else. Before 1973, R. beccarii was the only one of these three known to occur on the island. There were few specimens in collections of museums, no information about its natural history, and only speculations about its relationships to other species of rats. Students of Asian rats and mice have suggested that R. beccarii was related to R. cremoriventer, a forest species of the Asian mainland and islands on the Sunda Shelf. To test this supposition more specimens and natural history data about R. beccarii were needed and the species-limits of R. cremoriventer had to be defined. Four years ago I recorded aspects of the taxonomy, morphology, and geographic distribution of R. cremoriventer and its close relative R. langbianis (Musser, 1973). Then I traveled to Celebes where I hoped to obtain more information about R. beccarii, so I could later compare the species with its possible relatives west of Wallace's Line.

There was another genus of small rats that I thought might be related to *Rattus beccarii*. This was *Limnomys*, which consisted of three species represented by a total of five specimens. All came from mountains on the islands of Mindanao and Mindoro in the Philippines. While I was studying *R. cremoriventer* I had looked at these examples of *Limnomys*. Because of the morpho-

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logical similarity of some of the specimens to R. beccarii and because of their geographic origin, it was possible that they were relatives of R. beccarii and perhaps more closely related to that rat than was R. cremoriventer and its allies. But I did not then have time to study the few specimens of Limnomys carefully. And there were problems with the genus: three species had been described in the literature; two were similar to each other and resembled R. beccarii; and the third was so different that it raised questions as to the morphological limits and composition of Limnomys.

After I returned from Celebes in 1976 I spent three weeks at the National Museum of Natural History, Smithsonian Institution, where I studied the specimens of Limnomys and found answers to some of my questions about that group. The genus probably consists of only one species, not three, and one of the holotypes is a composite in which the skin is that of a Rattus, and the skull is from a Limnomys. My intention in the present paper is to provide some background about Limnomys, to identify the species that make up the composite holotype, and to discuss the composition of the genus. I report here results that are preliminary to a study that compares Limnomys with the three beccarii-type arboreal rats from Celebes.

Specimens I refer to in the following pages are in collections at the British Museum (Natural History) (BM) and the National Museum of Natural History, Smithsonian Institution (USNM). I am grateful to the staffs of those institutions for their help, especially Mr. John Edwards Hill (British Museum), Dr. Henry W. Setzer (Natural Museum of Natural History), and Dr. Don E. Wilson (National Fish and Wildlife Laboratory). Dr. Alfred L. Gardner (National Fish and Wildlife Laboratory) photographed the skulls depicted in figure 1; I appreciate his time and effort. Several of my colleagues and friends have read the manuscript. I thank them for their time and for their intelligent criticisms and suggestions for changes that have improved the report. The late Mr. Richard Archbold of Archbold Expeditions Inc., and the Council of the Scientific Staff of the American Museum of Natural History provided financial support for my studies in museums. The Celebes Fund of the American Museum of Natural History supported my field work in Celebes. The Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences) and Dr. Sampurno Kadarsan, Director of the Museum Zoologicum Bogoriense, sponsored my work in Celebes. I am grateful for their assistance and cooperation.

LIMNOMYS

The genus Limnomys was proposed by Mearns in 1905 and the type-species, L. sibuanus, was based on one specimen. In 1913 Hollister named and described two more species of Limnomys: L. mearnsi, known by three specimens and L. picinus, represented by only the holotype.

The type-species was described from the skin and skull of an adult female (USNM 125228). Mearns caught the rat on June 30, 1904, at 6600 feet on Mount Apo in southeastern Mindanao. In his original description of the species he wrote (1905, p. 452) that, "The unique type was trapped on a wet, mossy growth of vegetation, on the left bank of a little stream which in its lower course becomes the Sibuan River, flowing from Mount Apo. In spite of persistent efforts we failed to procure other specimens." That specimen is still the only example of L. sibuanus from Mount Apo.

Limnomys sibuanus is a small, long-tailed rat (table 1). Top and sides of the head and body are covered with tawny, dense, and long pelage (hairs are up to 13 mm. long); long, black guard hairs (up to 25 mm. long) are scattered over the back and rump. Underparts of the head and body are cream. The ears are dark brown. The tail is dark brown on all surfaces and is densely haired. The front and hind feet are brownish white and the hind feet have a dark brown strip from each ankle to bases of the digits. The hind feet are short and broad, similar in configuration to those of Rattus cremoriventer (see Musser, 1973). Six large and conspicuous teats are on the skin: one postaxillary pair and two inguinal pairs. Judged by their large size they were probably functional when the animal was alive.

The skull is small (table 1; fig. 1). The rostrum is short relative to the length of the rest of the skull. Each zygomatic plate is narrow. The brain-

TABLE 1
External, Cranial, and Dental Measurements (in Millimeters) of *Limnomys* in the National Museum of Natural History

	L. sibuanus	144622 ^b	L. mearnsi 144620 ^c	144621
	125228^{b}	young	young	young
	adult	adult	adult	adult
Measurement ^a	Q.	Q.	đ	Q
Length of head and body	125	87	105	102
Length of tail	150	133	136	138
Length of hind foot	30	27.5	29	28.5
Length of ear	21	18.5	20	20
Scale rows of tail (per cm.)	14	15	14	14
Greatest length of skull	33.2	28.5^d	29.8	_
Zygomatic breadth	16.2	14.5	15.2	_
Interorbital breadth	4.9	4.5	4.7	4.8
Length of nasals	11.1	10.0^{d}	10.4	10.6
Length of rostrum	9.4	8.2^d	8.9	8.6
Breadth of rostrum	5.8	4.8	5.2	5.3
Breadth of braincase	14.8	14.0	14.4	_
Height of braincase	10.1	9.7	9.9	_
Breadth of zygomatic plate	2.7	2.3	2.4	2.2
Depth of zygomatic notch	1.1	1.1	1.3	1.3
Breadth across incisor tips	1.5	1.4	1.4	1.4
Length of diastema	8.3	6.4	6.8	6.7
Palatal length	16.3	13.5	14.5	14.2
Palatilar length	13.9	11.7	12.6	12.2
Postpalatal length	11.6	9.3	9.8	_
Length of incisive foramina	6.2	5.4	5.4	5.5
Breadth of incisive foramina	2.1	1.9	2.0	2.1
Length of palatal bridge	5.8	4.5	5.0	4.9
Breadth of palatal bridge at M ¹	3.0	2.3	2.7	2.5
Breadth of palatal bridge at M ³	3.7	3.1	3.4	3.1
Breadth of mesopterygoid fossa	2.3	2.0	2.0	2.3
Length of bulla	5.6	5.0	5.7	
Breadth of bulla	5.5	5.2	5.2	
Height of bulla	4.6	4.6	4.6	_
Alveolar length of M ¹⁻³	5.0	5.2	5.4	5.3
Length of M ¹	2.3	2.4	2.5	2.5
Breadth of M ¹	1.5	1.7	1.8	1.8

^aExternal measurements were taken by E. A. Mearns in the field. Cranial and dental measurements were taken with dial calipers used beneath a dissecting microscope. Limits of most of those dimensions measured are explained in Musser (1970).

d_{Estimated} figures; about 0.5 mm. of the tips of the nasals are missing.

case is large and round. The incisive foramina are short. The bony palatal bridge is short and wide. The molars are small. Each is worn but parts of the occlusal patterns are still visible.

Eight years after Mearns's description of Limnomys sibuanus was published, two new species were added to the genus, both named and described by Hollister in 1913: L. mearnsi and

b Holotypes.

^cCranium and mandibles of specimen were associated with USNM 144605, the holotype of *Limnomys picinus*, but really belong with the skin of USNM 144620, (see text).

L. picinus. Hollister described L. mearnsi from three specimens obtained by Mearns from Grand Malindang Peak, elevation 9000 feet. This peak is part of a mountain complex about 145 air miles northwest of Mount Apo in the western portion of Mindanao. All three specimens were collected on June 6, 1906 (Hollister wrote June 7, but Mearns clearly indicated in his field catalogue that the specimens were collected on June 6). Hollister selected USNM 144622 as the holotype. He thought it was an adult. His diagnosis was, "Size small; coloration much darker than in Limnomys sibuanus, upperparts more slate-gray, less reddish; underparts whitish, not buffy. Skull much smaller, with larger teeth." He continued with the color as, "Upperparts an indefinite dull grayish-brown, the pelage long and soft, deep neutral gray, tipped with dull brown; sides paler; underparts entirely whitish, the hairs unicolor. Hands thinly haired with white; feet blackish, edged with white; toes white." The skull and teeth were described as "Skull much smaller than that of L. sibuanus, with relatively wider and much more rounded braincase; supraorbital beading very slight. Teeth larger, relatively wider and much more rounded, m¹ specially wider and less narrowed anteriorly." Hollister also listed a few external and cranial measurements of the holotype. The three specimens of L. mearnsi, USNM 144620, 144621, and 144622, are smaller versions of L. sibuanus. The upper parts are grayish brown instead of tawny, the underparts are white instead of cream, the fur is shorter and the inconspicuous black guard hairs barely extend beyond the overhairs (table 1); otherwise, specimens of the two forms are similar. The skull of the holotype of L. mearnsi also resembles that of L. sibuanus: it differs in absolute size of some dimensions and in some proportions that are related to differences in age (fig. 1). Hollister correctly assessed the affinities of the two sets of specimens by describing mearnsi as a form of Limnomvs.

Although Limnomys sibuanus and L. mearnsi resemble each other, the other species described by Hollister (1913, p. 325), L. picinus, is very different. It was based on one specimen identified by Hollister as an adult female, and was obtained by Mearns on November 16, 1906 from

the spur of the main ridge of Mount Halcon in Mindoro at an elevation of 4500 feet. Hollister diagnosed the taxon as "Size medium; tail and ears short; coloration wholly different from the other known members of the group, blackish above, dusky below. Pelage long and very soft." He went on to describe the color as "Above blackish, the head, forward part of body, and sides finely lined with ochraceous-buff. The hairs are uniformly dark neutral gray, with narrow tips of ochraceous-buff. Scattered through the pelage of back are numerous overlying hairs of pure black, which greatly reduce the effect of the ochraceous tips on the ordinary hairs. Center of back and rump almost pure blackish; cheeks lighter, more gravish-buff. Underparts dark grayish-drab, not sharply marked from color of sides, the hairs gray at bases, tipped with drab. Hands and feet brownish-black, the digits with long yellowish-white hairs; tail brownish-black above, slightly lighter, more brownish, below." The skull and teeth were noted as "Skull smaller than that of L. sibuanus, larger than in L. mearnsi; in general shape more like that of mearnsi, with wide, rounded braincase and indistinct beading. Teeth slightly larger than in mearnsi; much larger than in sibuanus." And at the end of the description Hollister wrote, "This species is so different in color from the other two known forms of Limnomys that no direct comparison is necessary."

The skin of Limnomys picinus is strikingly different from skins of the other two species. It is from a small, blackish brown rat with a short, thinly haired tail, shorter in length than the length of head and body. Limnomys sibuanus and L. mearnsi are tawny or grayish brown rats with cream or white underparts and brown, hairy tails that are much longer than lengths of heads and bodies. At a first glance, the skin of L. picinus seems so different from the other specimens that you wonder why Hollister described it as a species of Limnomys. The skull and teeth, however, closely resemble skulls and dentitions of L. mearnsi and possibly Hollister used these features to place picinus in Limnomys.

I know of no other *Limnomys* that are in collections of museums, either in the United States or elsewhere. If there are any, they are

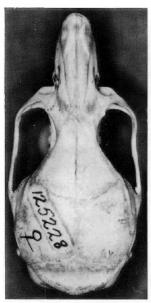












FIG. 1. Views of crania. Top: holotype of Limnomys sibuanus, USNM 125228. Bottom: holotype of L. mearnsi, USNM 144622. Approximately $\times 2$.

either sequestered under misidentifications or have been collected only very recently. The information now available about the genus and its composition derives from study of the specimens in the National Museum of Natural History. Two of the three samples are composites and must be sorted out before we can understand anything about the true nature of *Limnomys*.

THE MIX-UP AND IDENTITY OF LIMNOMYS PICINUS

In the late 1960s when I was well into a study of the taxonomy and zoogeographic relationships between species of rats and mice from the Asian mainland and those from the Philippine Islands and areas throughout the Indonesian Archipelago to New Guinea and Australia, I spent several

periods at the National Museum of Natural History, Smithsonian Institution, in Washington, D.C., where I worked through their large collections. I examined the holotypes of Limnomys and other specimens that had been allocated to that genus, but I remained perplexed about the nature of the genus and the species that composed it. There were only five specimens available. At least one skin of Limnomys mearnsi, not the holotype, was matched with a skull that seemed to be from a species of Apomys. And the skin of the holotype of L. picinus, so different from the skins of other Limnomys, was associated with what appeared to be a skull of L. mearnsi. Because other segments of the Asian fauna were receiving most of my attention at the time, I postponed working on Limnomys and did no more to unravel any possible mix-ups or to define limits of the species in the genus.

In the Fall of 1976, I traveled again to the National Museum explicitly intending to learn more about Limnomvs because I had found three species of small rats in Celebes that were more similar in morphology to some of the specimens identified as Limnomys than to any other kind of rat that I was familiar with. I had to answer the question: just what is Limnomys? It did not take long to see that one of the specimens of L. mearnsi was mismatched with a skull from a specimen of Apomys, and that the skull which should have been associated with the skin of L. mearnsi had been incorrectly placed with a skin of a juvenile Rattus mindorensis. These last elements constituted the strange holotype of L. picinus, and the mix-up involved elements of three genera.

The holotype of *Limnomys sibuanus*, the type-species of the genus, is no problem. The skin is correctly associated with the cranium and mandibles. The skin is prepared well and is in good condition. The cranium and mandibles are complete. The specimen is an adult rat and, except for *L. mearnsi*, represents a species that is unlike anything else now known from the Philippine Islands.

The three skins of *Limnomys mearnsi* are poorly prepared but in good condition. All are about the same size, seem to be from animals of about the same age, and because of these close resemblances could even have been from the

same litter. Each skin has two labels attached: one is a small rectangular paper tag with Mearns's field number written on it; the other is a museum label on which the place and date of capture are recorded. Each of the museum labels was added after the specimens reached Washington and after they were catalogued. Each of the skulls has only a museum label and none of the small field labels. The skull of the holotype (USNM 144622) consists of a cranium and mandibles; both elements are intact except for the tips of the nasals which were broken off and are missing. A second specimen, USNM 144621, seems to be associated with the correct skull; at least the skull is closely similar to that of the holotype, not only in size and configuration, but in approximate age. It is not in as good a condition: sections of the zygomatic arches, most of the braincase, and both bullae are missing.

On the museum label attached to the third specimen of L. mearnsi, USNM 144620, is the handwritten notation, "Skull not found." But there is now a skull associated with that skin and it is very different from skulls of the other two examples of L. mearnsi. The skull bears the same catalogue number as the skin, and there is a museum label in the vial bearing the same number and data. The skull is from an adult rat and is in fragments; only the front half of the cranium is complete. It is from a specimen of Apomys, not Limnomys. The name, "Apomys," had been typed on the museum label that was in the vial with the skull. Someone had also added a question mark in pencil after that name and the inquiry, "Limnomys?" Someone else had inserted a note in the vial on which "Skin of this number is a Limnomys" was written.

Apomys is the generic name proposed by Mearns (1905) for a group of species that he had collected from the high slopes of Mount Apo in southern Mindanao. Mearns named and described three species: hylocetes and insignis, based on small series from 6000 feet, and petraeus, known by two specimens from 7600 feet. Later, additional samples from Mindanao and other islands in the Philippines were named and described as species by Miller (1910), Hollister (1913), Sanborn (1952), and Johnson (1962). This group of mice lives in forests and is known only from Luzon, Catanduanes, and Mindanao in the

Philippine Islands. For more than 40 years mammalogists recognized *Apomys* as a genus distinct from *Rattus*, but in 1947 Ellerman reduced it to a subgenus of *Rattus* and this allocation was later followed by Simpson (1945) and Sanborn (1952). Persons who have worked more recently with specimens of *Apomys* now consider it to be a distinct genus that is not closely related to *Rattus* (Johnson, 1962; Misonne, 1969; Musser, 1977).

In 1906, when Mearns worked in the Malindang Mountains of Mindanao (which include Mount Bliss, Grand Malindang Peak, and Mount Lebo), he obtained series of one kind of Apomys. This sample was later named and described by Miller (1910) as Apomys bardus. Later, Hollister (1913) reduced bardus to a subspecies of A. insignis, a species originally described from specimens taken by Mearns on Mount Apo (Mearns, 1905). I have examined the holotype and other skins and skulls of bardus that were collected by Mearns (Mount Bliss, 5750 and 6000 feet, USNM 144826, 144581-144586; Mount Lebo, 5750 feet, 144579 and 144580; Grand Malindang Peak, 6100 and 900 feet, 144589-144592) and I agree with Hollister's allocation of the taxon; it is a geographic variant of A. insignis and closely similar in morphology to the samples of that species from Mount Apo. The skull now associated with the skin of the third specimen of Limnomys mearnsi is an example of Apomys insignis bardus. After I had determined this identity I looked through the entire series of skins and skulls of bardus that were collected by Mearns in 1906. With one exception, all the skins of bardus are matched with skulls of that form. The exception is an adult female, USNM 144591, one of two specimens taken at 9000 feet on Grand Malindang Peak on June 6, the same elevation and date as the specimens of Limnomys mearnsi. The skin is an adult example of A. i. bardus, the skull is not. The skull is in fragments and is from a juvenile of a species of Rattus, but not that of Rattus exulans, R. rattus mindanensis, R. argentiventer, or any other species known to occur in Mindanao; it is Rattus mindorensis, a forest rat restricted to the highlands of Mindoro Island in the central Philippines.

The skull now associated with that third

specimen of *Limnomys mearnsi*, USNM 144620, really belongs with the skin of *Apomys insignis bardus*, USNM 144591, and the skull now matched with the skin of *bardus* belongs to only one other skin—the holotype of *L. picinus*.

The skin of the holotype of Limnomys picinus, USNM 144605, is in good condition. Three labels are attached to it. One is a small rectangular paper tag bearing Mearns's field number, 6311. Two others are museum labels, one a regular label with date and locality of capture, the other a red type-label. The skull has no small tag with Mearns's field number associated with it, only a regular museum label and a typelabel. The cranium and mandibles are complete. That skull is an example of Limnomys mearnsi and resembles the other two skulls of L. mearnsi in size, configuration, and approximate age; it is the skull that should accompany USNM 144620, the skin of L. mearnsi that was matched with a skull of Apomys insignis bardus.

The skin of *Limnomys picinus* is simply a juvenile example of *Rattus mindorensis*, a taxon named and described by Thomas in 1898. The original series of five specimens (BM 97.5.2.28, 97.5.2.26, 97.5.2.25, 97.3.1.5., and the holotype, 97.3.1.4) were obtained by John Whitehead in December 1895, from Mount Dulangan, Mindoro at elevations of 1600 and 1650 meters. Those were the only specimens available for study in museum collections until Mearns collected 10 of these rats in 1906.

From at least March until sometime after the middle of July 1906, Mearns worked in Mindanao and it was during that period that he obtained the samples of *Limnomys mearnsi* from the Grand Malindang Mountains. By the first part of November he was in Mindoro and from the middle to nearly the end of November he lived and worked on Mount Halcon. There he collected 10 specimens of *Rattus mindorensis* from forest along the spur of the main ridge of Mount Halcon. All were prepared in the field as conventional study skins with dry skulls. Other data about these specimens important to my discussion here are listed in table 2.

Mearns knew about Rattus mindorensis. Along with his field catalogue and other papers I found a reference to Thomas's original description of R. mindorensis and descriptive notes that

	TABLE 2
	Mearns's Specimens of Rattus mindorensis from Mount Halcon, Mindoro
_	

USNM Catalogue Number	Mearns's Field Number	Sex	Age	Elevation (Feet)	Date Collected (Nov. 1906)	Deposition
144603	6309	male	adult	4500	15	Exchanged with Bureau of Science, Manila, May, 1936
144604	6310	female	adult	4500	15	USNM
144605	6311	female	juvenile	4500	16	USNM; skin is holotype of Lim- nomys picinus
144606	6314	male	adult	4500	17	USNM
144607	6315	female	adult	6300	18	USNM
144608	6318	male	adult	6300	18	Gift to Bureau of Science, Manila, Feb. 5, 1923
144609	6319	male	adult	6300	18	USNM
144610	6320	female	adult	6300	19	USNM
144611	6325	male	adult	6300	23	USNM
144612	6326	male	adult	6300	25	USNM

Mearns had written, presumably so he could recognize the rat if he caught it on Mindoro. Catch it he did, and with each specimen Mearns noted in his field catalogue the identification, "Mus mindorensis" and indicated whether the animal was adult or juvenile. After the specimens arrived at the National Museum of Natural History in Washington, D.C., they were catalogued in sequence of Mearns's field numbers and were all identified as "Mus mindorensis" (at that time the generic name Mus was used to embrace species of rats and mice that are now placed in Rattus) in the museum catalogue. For some reason Hollister (1913, p. 319) later reported on 11 specimens obtained by Mearns from Mount Halcon, but Mearns clearly collected only 10.

The seven adults of Rattus mindorensis in the National Museum of Natural History represent a medium-sized, dark brown rat. It is larger than R. exulans and smaller than either R. argentiventer or R. rattus mindanensis, the other three species of Rattus common to Mindoro. The pelage of R. mindorensis is dense, short (overhairs are 10-15 mm. long; guard hairs extend up to 30 mm.), and soft, with a woolly appearance, especially on the underparts of the head and body. Upper parts of the head and body are dark to blackish brown, highlighted with chestnut. The ears are dark brown and scantily haired. The front and hind feet are also brown. The tail is

dark brown everywhere and has 9 or 10 rows of scales per cm. Underparts of the head and body of most specimens are dark gray washed with pale buff; one specimen has dark, slate-gray underparts. Female have 10 teats: a pectoral pair, one postaxillary pair, one abdominal pair, and two inguinal pairs.

Of the other species of Rattus that live on Mindoro, R. mindorensis might be confused only with the Philippine house rat, R. rattus mindanensis. That is a much larger animal, having a thinner pelage, appearing sleek rather than dense and woolly. The upper parts are buffy brown instead of blackish brown. The feet are paler, and range from brownish gray to brown. The underparts of head and body are variable in color. One extreme is white or cream underparts sharply demarcated from the head and back; the other is buffy brown underparts that resemble the upper parts in hue; most specimens fall between these limits and have whitish or buffy gray underparts. And, R. rattus mindanensis has a larger skull and teeth than in R. mindorensis.

The skin of the holotype of *Limnomys* picinus is from a small rat (length of head and body, 105 mm.; length of tail, 100 mm.; and length of hind foot, 28 mm.). The pelage is dense, fine, woolly and short (overhairs extend to 9 mm.; guard hairs to 15 mm.). Upper parts of the head and body are blackish brown; under-

parts are gray with a pale buffy tinge. The ears, feet, and tail are dark brown. The tail is scantily haired and has small scales, 15 rows per cm. The skin is from a juvenile of *Rattus mindorensis*. The short, soft, and fine pelage is typical of juvenal pelage. So, too, is the short tail with its small scales, and the other small dimensions of the skin. This skin is the specimen that Mearns had identified as a juvenile "Mus mindorensis" in his field catalogue under the number 6311 and is the only juvenile specimen of the 10 rats (table 2). The skull that goes with this skin was mismatched with the skin of *Apomys insignis bardus*, USNM 144591.

The skull of USNM 144591 is in fragments; only the front half of the cranium and the mandibles are whole. The upper and lower first and second molars had erupted when the rat was caught, but the third molars had not. In 1906 Mearns collected samples of both R. rattus mindanensis and R. exulans from Mindoro, and I examined the skins and skulls of these specimens to be certain that the skull of USNM 144591 did not belong to these species. All the skins of those species were associated with the right skulls. I then compared the skull of USNM 144591 with adults and juveniles of R. mindorensis and R. rattus mindanensis. Because the skull is badly fragmented I compared dimensions and cusp patterns of the erupted first and second upper molars with teeth of the other two species. The teeth of USNM 144591 are smaller than in specimens of R. rattus mindanensis and fit with the examples of R. mindorensis. For example, for seven specimens of R. mindorensis (USNM 144603, 144606, 144607, 144609 and 144610-144612) the crown lengths of the first two upper molars range from 4.7 to 5.2 mm., length of the first upper molar is 2.9-3.3 mm., and breadth of that tooth is 1.8-2.0 mm. The range for the same dimensions of seven R. rattus mindanensis (USNM 144623, 144624, 144628, 144530, 278559, 277674, 283852) are 5.1-6.1 mm., 3.1-3.9 mm., and 2.1-2.3 mm. Values for USNM 144591 for the same dimensions are 5.1 mm., 3.3 mm., and 1.8 mm.

I also compared the dental measurements of USNM 144591 with 20 adult specimens of Rattus exulans from Mindoro (USNM 277554, 277555, 277583-277586, and 277640-277653).

In that series, crown lengths of the first two upper molars range from 3.6 to 4.4 mm., and the lengths and breadths of the first upper molars range, respectively, from 2.3 to 2.7 mm., and 1.5 to 1.7 mm.; all values are clearly smaller than those from USNM 144591. Finally, the cusp patterns of the erupted molars of USNM 144591 are like those in young adults of *R. mindorensis* in the Mearns series that have little wear on the teeth.

I regard only the skin of USNM 144605 to be the holotype of *Limnomys picinus* Hollister, 1913. That scientific name becomes a subjective synonym of *Mus mindorensis* Thomas, 1898, a valid species in the genus *Rattus*. The skull now associated with the skin of USNM 144605 should be rematched with the skin of *Limnomys mearnsi*, USNM 144620, and the skull presently numbered USNM 144620 should be considered part of specimen USNM 144591, *Apomys insignis bardus*. Finally, the skull originally matched with the *Apomys* skin of USNM 144591 should be associated with the skin of USNM 144605, the holotype of *L. picinus*.

Mearns was a good collector and the lots of specimens he shipped from the Philippine Islands still form a significant base of knowledge about that rich and diverse fauna of mammals in general, and rats and mice in particular. But he apparently had trouble keeping skins and skulls properly labeled in the field so they could be correctly associated later in the museum. And in the museum, Hollister, who studied most of Mearns's collections, apparently did not realize that some skins were incorrectly matched with particular skulls. For example, in the same paper in which Hollister described L. picinus, he also named and described Epimys benguetensis. That taxon, based on a specimen collected by Mearns in 1907 from the Benguet Province of Luzon, is also a composite and I have identified the elements that comprise it elsewhere (Musser, 1977).

Perhaps it is graceless to single out Hollister and isolate him as describing taxa of rats from specimens in which the skin was a different species than the skull associated with it. Others have made similar mistakes. In 1941 Sody described two new rats from Celebes. The species were so unique they were never collected again;

nor could the names be tied to specimens in collections of museums. The reason: each holotype was a composite of species already named and described (Musser, 1971). In his monograph on the mammals of Chile, Osgood (1943) pointed out that *Chelemyscus*, a genus proposed by Oldfield Thomas for a Chilean mouse, was likely based on a composite holotype. And just recently, Bishop (1974) has discussed the identity of an Indian mouse in which the holotype consisted of the skin of one species and the skull of something else. But, considering the hundreds of holotypes and names tied to them, such mistakes noted above are, fortunately, rare.

THE SPECIES IN LIMNOMYS

With the identification of *Limnomys picinus* as a composite there remain only two other named forms in Limnomys, the type-species, L. sibuanus, and L. mearnsi. In most external, cranial, and dental features the three specimens of L. mearnsi are simply small versions of L. sibuanus. The differences between the two samples seem to me to be a reflection of age more than of features that distinguish two species. I think the three specimens of L. mearnsi are immature examples of L. sibuanus. Hollister (1913) thought they were adults. The oldest specimen of the lot is USNM 144620. It is in fresh pelage and appears to me to have just completed the molt from juvenal into adult pelage when it was caught. The other two specimens are also covered with fresh pelage, but new hairs were still proliferating over parts of the back and sides of each when they were caught. In many species of small rats the new adult pelage is always shorter and duller than in specimens of older and usually sexually mature adults. Pelage of the younger rats feel softer and the guard hairs barely extend beyond the overfur, making them inconspicuous when compared with the long, black guard hairs of older adults. The differences in tone, length, and texture of pelage between the holotype of L. sibuanus and the three specimens of L. mearnsi are those kinds of differences I have noted between adults and very young adults in other species.

Another indication of the young age of the three specimens of *L. mearnsi* is that two of them are female but nowhere on the skins can I

locate any teats. The animals were either sexually immature or they were incorrectly sexed. The latter is less likely because Mearns sexed all specimens in the field and judging from his data from other samples he was careful to determine the correct sex.

Color and hairiness of the tails of *L. mearnsi* also point to young animals. In all three specimens the tails are grayish brown and the hairs are much shorter than in the dark brown, longhaired tail of *L. sibuanus*. In other rats with such pigmented, hairy tails, the color darkens with age and the hairs increase in length.

Differences between skulls of the two samples are those associated with different age groups. All three skulls of L. mearnsi have a short rostrum, large and inflated braincase with no ridges bordering the frontals and parietals, and slightly worn teeth. With increase in age the rostrum lengthens, the braincase lengthens and loses some of its globular configuration, ridges bounding the dorsolateral margins of the frontals and parietals appear and gradually become more prominent, and the teeth wear down. All three skulls of L. mearnsi are small disproportionate versions of the skull of L. sibuanus (fig. 1) and with a change in the proportions as the skulls became larger they would closely resemble the skull of L. sibuanus. The only feature that may differ between the two samples is length of the molar row. It is shorter in L. sibuanus (table 1).

The similarity of the rat faunas between Mount Apo and the Grand Malindang Mountains also suggest that L. mearnsi is at most a geographic variant of L. sibuanus. In addition to the specimens of L. mearnsi, two other kinds of small forest rats, Tarsomys apoensis and Apomys insignis, have been taken in the mountain forests of both places (Hollister, 1913). There are perhaps too few specimens of Tarsomys (two from Grand Malindang Peak, two from Mount Bliss and one from Mount Apo) to assess any possible geographic variation, but to me all the specimens look like the same kind of rat. The series of Apomys insignis from each place are larger than those of Tarsomys, and though the sample from the Grand Malindang Mountains is recognized as a subspecies, A. i. bardus, the differences in features of skins and skulls between it and the sample from Mount Apo are, as Hollister (1913) indicated, slight.

I suspect that the four known specimens of Limnomys represent but one species, with possible geographic variants. For now, I regard the taxon mearnsi as a subspecies of L. sibuanus. True, I have not seen young examples of L. sibuanus from Mount Apo, nor mature adults from the Grand Malindang Mountains, but as I noted above, the differences between the two available samples are those that I have found between adults and very young adults in other species of rats that appear to be related to Limnomys and many kinds that are not closely related to that genus.

DISCUSSION

Limnomys has been listed as a genus in the mammalogical literature from 1905 until 1945 but its distinction relative to the genus Rattus was questioned only two years after Mearns's original description was published. In 1907 Oldfield Thomas reported on a small collection of mammals obtained by M. P. Anderson in Mindanao. Anderson's intention was to collect samples of the same species from Mindanao that had been described by Mearns in 1905. He was successful only in obtaining a specimen of what Mearns had described as Bullimus bagobus. Thomas did not think that Bullimus was distinct from Mus, the generic name used at that time for species now included in Rattus, and he wrote that, "It is unfortunate that Dr. Mearns had not had experience of the difficulties of Murine dental characters before venturing to describe genera of this group. Had he had such experience I am sure he would not have described Bullimus, nor would he have based another genus (Limnomys) on a single specimen with teeth 'too worn to furnish characters distinguishing them from Mus,' unless the other characters were of a more striking nature than appears from his account."

Later Ellerman (1941) was equally skeptical about the generic validity of *Limnomys*. He listed it as a separate genus in his classical work on the families and genera of living rodents, but under the account of *Limnomys* he noted that, "From the original description, this genus has not a single character to distinguish it from *Rattus*. This conclusion is apparently reached by Thomas. ..." Four years later Simpson

(1945) included *Limnomys* in *Rattus*; likely he was influenced by Ellerman's published opinion. Finally, in 1951 Ellerman and Morrison-Scott included *Limnomys* in their list of generic synomyms within *Rattus*.

Misonne's (1969) report on evolutionary trends in African and Indo-Australian Muridae is another important work on murid rodents. In it he did not write about *Limnomys* because he had not seen any specimens, but he still included that genus within Rattus in his list of genera at the end of the paper. And neither Thomas, Ellerman nor Simpson had ever examined specimens of Limnomys. Their opinions were formed from published descriptions and the only available accounts were those by Mearns (1905), Hollister (1913), and Taylor (1934). Mearns's original description of the genus was not diagnostic and it is difficult to obtain an accurate image of the included species and its relationship to other murids. Hollister's descriptions of L. mearnsi and L. picinus were equally unclear as far as trying to assess the relation of Limnomys to other genera was concerned, and Taylor's accounts were taken from the descriptions of Mearns and Hollister.

I have examined the specimens of Limnomys but at this time I cannot offer a final assessment of the relationships between Limnomys and Rattus. The problem is that the genus Rattus has yet to be finally diagnosed and defined. Different investigators have had different opinions about the content of that large genus. For many years Ellerman's (1941, 1949, and 1961) view, expressed by bringing together a large number of African, Indian, and Asian species with a great range of morphological diversity, prevailed and was accepted by everyone. By the end of 1961 40 generic names were included within Rattus (Sody, 1941; Ellerman and Morrison-Scott, 1951, 1955; Ellerman, Morrison-Scott, and Hayman, 1953; Sanborn, 1952; Ellerman, in Laurie and Hill, 1954; Ellerman, 1961). Missone's work, published in 1969, resulted in a different view of the contents of Rattus. It is instructive to compare the two versions here. Below I list the genera that Ellerman and others included as either synonyms of Rattus or valid subgenera. Next to it is a list of the same genera but arranged according to Missone's interpretation (refer to the publications by Ellerman, 1941, 1949, 1961; and Mis-

Misonne		
AFRICAN		
Genus Praomys		
Myomys (? status)		
Subgenus Mastomys		
Subgenus Hylomyscus		
Subgenus Myomyscus		
Genus Aethomys		
Subgenus Micäelamys		
Genus Thallomys		
Genus Stochomys		
Genus Dephomys		
Genus Zelotomys		
Ochromys		
INDIAN		
Genus Millardia		
Grypomys		
Guyia		
Millardomys		
Subgenus Cremnomys		
Madromys		
2.22.0.		
ASIAN		
Genus Rattus		
Pullomys		
Mollicomys		
Geromys		
Cironomys		
Christomys		
Octomys		
Arcuomys		
Subgenus Stenomys		
Subgenus Leopoldamys		
Subgenus Bullimus		
Limnomys		
Tarsomys		
Tryphomys		
Bunomys		
Taeromys		
Berylmys		
Paruromys		
Frateromys		
Genus Lenothrix		
Genus Apomys		
Genus Maxomys		
Genus Diplothrix		

sone, 1969, for names of authors and dates of publication of the names; I have also omitted *Epimys* from the list, which is a name accepted by everyone as a subjective synonym of *Rattus*).

Based on his own studies and information in

the published literature, Misonne pointed out that many of the genera included within *Rattus* by Ellerman and other authors were actually valid, and some were not morphologically close to *Rattus* at all. To Misonne the scope of *Rattus*

is much narrower than that envisioned by Ellerman. Misonne's view of Rattus also spotlights interesting and significant zoogeographic patterns. For example, Ellerman's concept would include Rattus as a native element in the large African fauna of murid rodents. Misonne's narrower definition of that genus excludes it as a native African group and emphasizes the point that there are no indigenous African Rattus. The only species of true Rattus on the continent are R. rattus and R. norvegicus, species thought to be native to Asia and unintentionally brought to Africa by human transport.

Even with the exclusion of the African, Indian, and some Asian genera from Rattus, the genus still contains many species; Misonne has retained 18 generic names within it. From my own studies I think there are species and groups of species now included within Rattus that do not belong there. My approach to a definition of the genus has been to sort specimens into what appear to be real species, defining their limits from data of morphology and geographic distribution, the kinds of data usually available for most specimens. Grouping the species is the next step, looking to see where they fit morphologically in relation to species in other genera and to species that are included within the subgenus Rattus-the core of that large and complex group. I am still in that process and I cannot yet provide a satisfactory definition of Rattus. The information I have gathered indicates to me that the dimensions of the genus will be diminished from what it is now.

I do not want to elaborate further about the breadth and content of the genus Rattus in the present report. I only provide some background to illustrate the shifting dimensions of the genus through time and study, and the attendant difficulty of separating species from it or allocating genera to it. The murid faunas of Africa, India, and Asia are large and the interrelationships among the many species are complex. Except for a few peculiar species, the large core of rats and mice have historically been placed together in a huge group, and the taxonomic change through time has been one of gradually diminishing the size of the group as people looked more carefully at specimens and saw more important details. At first the large assemblage of species was embraced by the name Mus. That genus and its allies were later separated and the remainder brought together under the name Epimys, which was replaced by Rattus. During the time that Ellerman and his colleagues were active the genus Rattus was still large and contained more than 550 named forms, such an impressive assemblage that Simpson (1945, p. 89) called it "the most varied genus of mammals..." Now Misonne has given us a different concept of Rattus, less varied and more geographically restricted.

The genus Limnomys is a taxon that will probably be excluded from Rattus. Limnomys sibuanus is distinctive. The combination of short body, long and hairy tail, short and broad hind feet, six teats, short rostrum, narrow zygomatic plates, short bony palatal bridge, large bullae, and the details of molar topography reinforce Mearns's view that Limnomys is a valid genus, something outside the monophyletic radiation represented by the core of Rattus. If my interpretation of data obtained from the few specimens of Limnomys is correct, there is only one species in the genus with possible geographic variants. The rat lives in mountain forests and is now known only from Mindanao in the southern Philippines. It is part of that large and diverse murid fauna so peculiar to the Philippine Islands. Limnomys sibuanus may also have morphological ties to a group of three species on Celebes which includes what is now called Rattus beccarii.

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